

## Research Article

# The greater the proportion of *Robinia pseudoacacia* in a stand the greater its effect on the population characteristics of *Erythronium dens-canis*

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## Abstract

Management of invasive alien plants is an increasing problem throughout the world. In some cases native rare or protected species can appear or even prefer habitats dominated by invasive alien plants, which raises questions about the optimal treatment of such areas. *Erythronium dens-canis* in Hungary is a protected species which only have several occurrences in the country and a number of these populations situated in *Robinia pseudoacacia* stands developed after harvesting native forests. In this study a total of five populations of *E. dens-canis* were surveyed between 2020 and 2022 in southwestern Hungary examining and comparing the ongoing demographic changes under native and *Robinia* stands by monitoring individual plants. Two populations were situated in forests composed of native tree species, two in *Robinia pseudoacacia*-dominated stands and one in a *Robinia*-native tree species mixed stand. We categorized the plants into five age-state categories: dormant, seedling, juvenile, vegetative adult, and reproductive adult. We found some considerable differences (e.g. leaf size, reproduction rate) between the populations situated in native and in *Robinia* stands, whereas the population in mixed forest showed intermediate character in most examined factors. Based on our results, *R. pseudoacacia* have a significant effect on the phenology and life history of *E. dens-canis*, and this effect is greater with higher proportion of *R. pseudoacacia* in a forest stand where the *E. dens-canis* occurs.



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**Key words:** Endangered species, habitat transformation, Hungary, invasive alien species, population dynamics

## Introduction

One of the most problematic aspects of invasive alien plant species is their potential ability to transform ecosystems in which they are introduced to (Richardson and Rejmánek 2011). They can affect plant functional traits (Sitzia et al. 2018), influence community structure and composition (Daehler and Strong 1994; Hejda and Pyšek 2006; Gaertner et al. 2009; Nascimbene and Marini 2010) together with altering soil characteristics and nutrient cycling (De Marco et al. 2013; Medina-Villar et al. 2015). Biological invasions can lead to homogenization of native communities (McKinney and Lockwood 1999; Rooney et al.

2004), loss of biodiversity, including altered ecosystem functioning (Pimentel et al. 2001; Didham et al. 2007; Vilá et al. 2010).

In Hungary, *Robinia pseudoacacia* L. (black locust or false acacia) is one of the invasive alien plant species with the greatest impact on natural ecosystems (Mihály and Botta-Dukát 2006). *R. pseudoacacia* belongs to the legume family (Fabaceae), it is a light-demanding pioneer species native to North America. In its native range it rapidly colonises forest gaps and is gradually replaced by other tree species after 15–30 years. In contrast, in secondary habitats its populations can persist for longer periods, displacing native communities (Cierjacks et al. 2013) and therefore *R. pseudoacacia* is considered an invasive species throughout Europe, which resulted in the inclusion of this species in national blacklists and other lists summarising alien species (Norway: Gederaas et al. 2012; Czech Republic: Pyšek et al. 2012; Pergl et al. 2016; Germany: Seitz and Nehring 2013; Italy: Celesti-Grapow et al. 2009; Switzerland: FOEN 2010).

It was one of the first American tree species to be introduced to Europe in the early 17<sup>th</sup> century (Vadas 1914; Vítková et al. 2016) due to its numerous economically positive properties (Vadas 1914; Göhre 1952; Straker et al. 2015). Since then, *R. pseudoacacia* has played a major role in forest management in Hungary, resulting in a significantly higher proportion of black locust forests than in other Central European countries (Vítková et al. 2017). The share of *R. pseudoacacia* in the managed forested areas is the highest (nearly 460 thousand hectares, about 24%; KSH 2023) of all tree species, and its area is still increasing (KSH 2023).

Several authors have shown that the herbaceous level of *R. pseudoacacia*-dominated forests differs significantly from that of native forests in Europe (Wendelberger 1954; Montagnini et al. 1991; Peloquin and Hiebert 1999; Von Holle et al. 2006; Taniguchi et al. 2007; Vítková et al. 2016). Under the canopy of *R. pseudoacacia*, conditions are more favourable for shade-tolerant and nitrophilous species (Hruška 1991; Cierjacks et al. 2013; Vítková et al. 2016).

In the first half of the growing season, two different phenological aspects of the herb layer are observed in *R. pseudoacacia*-dominated forests (Vítková et al. 2017). In early spring, before the appearance of *Robinia* leaves (March-April) geophytes and ephemeral annuals are observed. In late spring (May-June), shade-tolerant annuals, common nutrient-demanding plants and grasses appear. In the second half of the growing season, annuals and geophytes disappear and the herb layer often dries out (Vítková et al. 2017).

As agricultural intensification in Europe resulted in substantial loss of natural habitats (Tilman et al. 2001), there has been a gradual selection towards species that can survive in secondary habitats or on the edge of cultivated fields, especially when the management is extensive (Perrino et al. 2014). This process, although in a slower pace, is still in progress, and therefore the conservational value of semi-natural habitats is gradually increasing, as for example for annual meadows of the *Thero-Brachypodietea*, that give refuge to some rare and endangered plant species (Brana et al. 2014; Perrino et al. 2022, 2023), and are considered a priority habitat of the Directive 92/43/EEC. In Hungary, several rare and endangered species occur in *Robinia*-dominated stands, such as *Erythronium dens-canis* L., *Crocus reticulatus* Steven ex Adams or *Sternbergia colchiciflora* Waldst. Et Kit. (Bagi et al. 1998; Pacsai et al. 2022). As *E. dens-canis* only has a few large populations in Hungary and a number of these are situated in

*Robinia* forests, the better understanding of the species biology and ecology in this specific situation is essential to plan suitable treatments of these habitats. Relatively little is known about the population biology of *Erythronium* species in general, a few long-term studies have been carried out so far with *E. japonicum* Decne. (Kawano et al. 1982) and *E. americanum* Ker Gawl. (Holland 1981), and two study concentrated on *E. dens-canis*, one in Italy (Pupillo and Astuti 2017), and one in Ukraine (Kricsfalussy et al. 1995) where the detailed morphological and demographic properties of multiple populations were monitored through five years.

In our study we started a long-term monitoring of five *E. dens-canis* populations occurring in forests with different compositions: natural forests consisting of native tree species, intermediate, mixed and semi-natural, *Robinia*-dominated stands to follow the demographic and structural changes taking place in each population. During the first year of the study we noticed considerable differences in phenology and demography of the *E. dens-canis* plants in native and in *Robinia* stands (significantly different-sized individuals in same age-states, different ratio of flowering and pollination), which prompted us to expand our study with more, intermediate type sites to investigate these differences between populations situated in these two types of habitats in more detail.

## Materials and methods

### The dog's tooth violet (*Erythronium dens-canis* L.)

*E. dens-canis* is a monocotyledonous, perennial geophyte species, belonging to the lily family (Liliaceae). Mature specimens of the species are 10–30 cm tall (Király 2009). It flowers before trees leafing out, starting in mid-February. The vegetative plants produce one leaf, reproductive ones produce two leaves, varying in shape from ovate to lanceolate, slightly fleshy, ashy green, with brown spots that fade by the end of the growing season (Király 2009; La Rocca et al. 2014). It produces its characteristic, pink (rarely white) flowers with recurved petals with dark purple (rarely yellow) stamens, usually solitary, on 8–25 cm peduncles. The fruit is a tricarpic capsule, in which the seeds ripen in May. The seeds have an elaiosome, which is dispersed by ant species (myrmecochoria) (Guitián et al. 2003). It occurs in dry to mesophilic, usually slightly acidic soils, in hornbeam-oak woodlands, beech woodlands, mountain meadows, less frequently in wet meadows, but mainly in older, more open forest stands (Király 2009, Vacek et al. 2020).

All members of the genus *Erythronium* are native to the northern temperate zone. In Europe, only one of them, *E. dens-canis* is native. In Asia, three more species [*E. caucasicum* Woronow, *E. sibiricum* (Fisch. & C.A.Mey.) Krylov and *E. japonicum* Decne.] are present, and 23 species occur in North America (Kawano 2005). Despite the fact that *E. dens-canis* is listed as a threatened species in several European countries [Hungary: near threatened (Király 2007), Austria: regionally endangered (Niklfeld and Schrott-Ehrendorfer 1999), Slovakia: vulnerable (Turis et al. 2014), Romania: vulnerable (Hurdu et al. 2022)] or only small local populations occur [Czech Republic (Vacek et al. 2020), Ukraine (Tykhonenko et al. 2017), Hungary (Nagy et al. 2019)], few studies have investigated the life history, ecology and population dynamics of the species (Kricsfalussy

and Mihaly 1993; Kricsfalusi et al. 1995; Gutián et al. 1999; Mondoni et al. 2012; Pupillo and Astuti 2017).

Similar studies have been carried out mainly on species occurring in America (*E. americanum*, *E. grandiflorum* Pursh) and Japan (*E. japonicum*) (Holland 1974; Muller and Bormann 1976; Yokoi 1976; Kawano et al. 1978; Holland 1980; Kawano et al. 1982; Hughes 1992; Ruhren and Dudash 1996; Sawada et al. 1997; Takada et al. 1998; Kawano 2005; Tessier 2019). As these species have similar life histories, they are occurring in similar habitats and genetically close to *E. dens-canis* (especially *E. japonicum*, which some authors describe as a subspecies of *E. dens-canis*), we used literature related to these species as well in the design and preparation of the present research.

### Study area and permanent plots

In 2020 we installed permanent quadrats (1×1 m) along transects at three locations (one near Becséhely and two near Lispeszentadorján villages) for long-term monitoring of *E. dens-canis* populations. The corners of these quadrats were marked with nails and numbered aluminium plates to ensure the accurate positioning of the 1×1 m frames (with 10 cm wire grids) which helped us in repeated locating of individuals. Two of the studied *Erythronium* populations situated in native forest stands (Native 1, Native 2: Lispeszentadorján 1 and 2; abbreviations: N1, N2) and one in a *R. pseudoacacia*-dominated, secondary forest (*Robinia* stand 1: Becséhely 1; abbreviation: R1). In 2021 two more set of permanent quadrats have been installed, one in a *Robinia*-dominated stand (*Robinia* stand 2: Becséhely 2; abbreviation: R2) whose population was discovered in 2020, and one in a stand composed of approximately half *Robinia* and half native tree species (Native-*Robinia* mix: Lispeszentadorján 3; abbreviation: NR) (Table 1). In each area, we installed enough quadrats (their number varied between 7 and 16 per site) to have included at least 100 individuals per sample area. The positions of each *Erythronium* individual within the quadrats were recorded by 1 cm accuracy and they were marked individually by nails equipped with numbered aluminium plates. This way we were able to find the same individuals repeatedly throughout the years.

Since it is very difficult to determine precisely the age of some bulbous species, demographic-population dynamics studies often classify individuals into age-state categories based on various physical parameters (Rabotnov 1985). In our study, we used methods commonly used for population dynamics studies of geophyte species and age-state classification based on leaf morphology

**Table 1.** Description of the sample sites.

| Sample sites and their abbreviations in parentheses | dominant tree species   | locality (WGS84, DD; X,Y) | elevation (m a.s.l.) | no. of censused plants between 2020 and 2022 (min–max) |
|---|---|---------------------------|----------------------|--|
| Lispeszentadorján 1 (N1)                            | <i>Quercus robur</i> , <i>Carpinus betulus</i>                    | 46.52987°N, 16.70998°E    | 225                  | 110–185  |
| Lispeszentadorján 2 (N2)                            | <i>Fagus sylvatica</i> , <i>C. Betulus</i>                        | 46.53225°N, 16.71440°E    | 220                  | 146–172  |
| Lispeszentadorján 3 (NR)                            | <i>Robinia pseudoacacia</i> , <i>C. Betulus</i> , <i>Q. Robur</i> | 46.52972°N, 16.71071°E    | 230                  | 80–104   |
| Becséhely 1 (R1)                                    | <i>R. pseudoacacia</i>  | 46.46072°N, 16.79269°E    | 210                  | 112–294  |
| Becséhely 2 (R2)                                    | <i>R. pseudoacacia</i> , <i>C. Betulus</i>                        | 46.46271°N, 16.78128°E    | 245                  | 276–396  |

measurements, which have been proven suitable for other *Erythronium* species (Yokoi 1976; Kawano et al. 1982; Sawada et al. 1997) as we assessed this method in our earlier study on *E. dens-canis* (Pacsai et al. 2022). We measured maximum length (without petiole) and width of each leaf of every individual (besides seedlings, as their length were recorded only), and presence or absence of reproductive organs at the end of the flowering period (April) between 2020 and 2022.

### Data analysis

Leaf area was estimated using a coefficient derived from proportions of leaf areas to leaf length and width ratio measured by image analysis of 76 leaves of 56 *E. dens-canis* individuals, photographed in 2020 at the study sites (Pacsai et al. 2022).

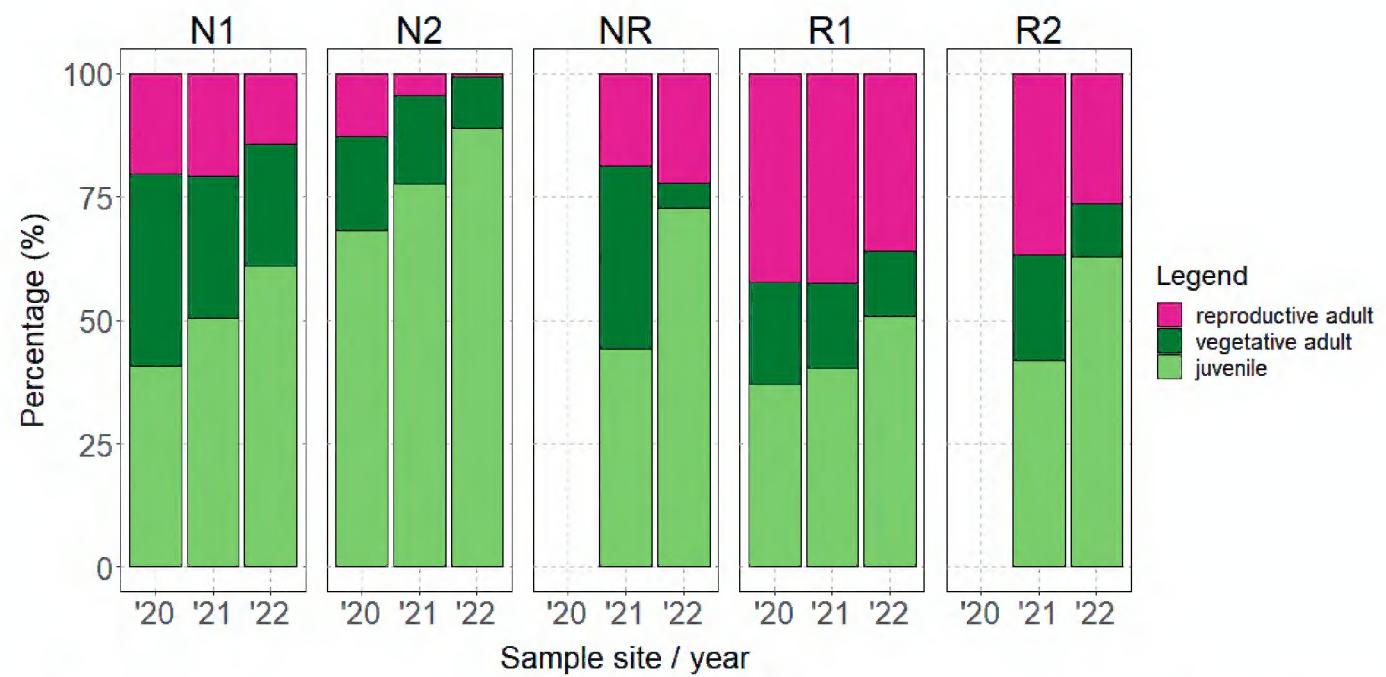
One of the main difficulties in the case of perennial species is the separation of juvenile individuals and vegetative adults. As we wanted to study the long-term life history of individuals of this species and it is also protected by law in Hungary, we used only non-destructive methods during the data collection. Therefore we couldn't examine the bulbs of the individuals which otherwise could have provided significant help in categorizing the plants into age-states (Kricsfalusi et al. 1995). We used leaf area of the smallest (but statistically not outlier) reproductive individuals as the boundary line between the juvenile and vegetative adult age-state categories. As the time of measurement and environmental factors affect plant growth, this limit should be estimated for each year and each site separately (Jeong et al. 2022; Pacsai et al. 2022).

Since it cannot be determined whether a plant is dead or dormant at this point (the possible length of the prolonged dormant period is not yet known), we considered dead only seedlings which did not appear in the following years. Beside these instances, we categorized the plants as dormant when they did not produce aboveground organs. Calculating population growth ( $\lambda$ ) without including mortality rates obviously results in skewed values, but it still makes it possible to compare each population with some certain limitations.

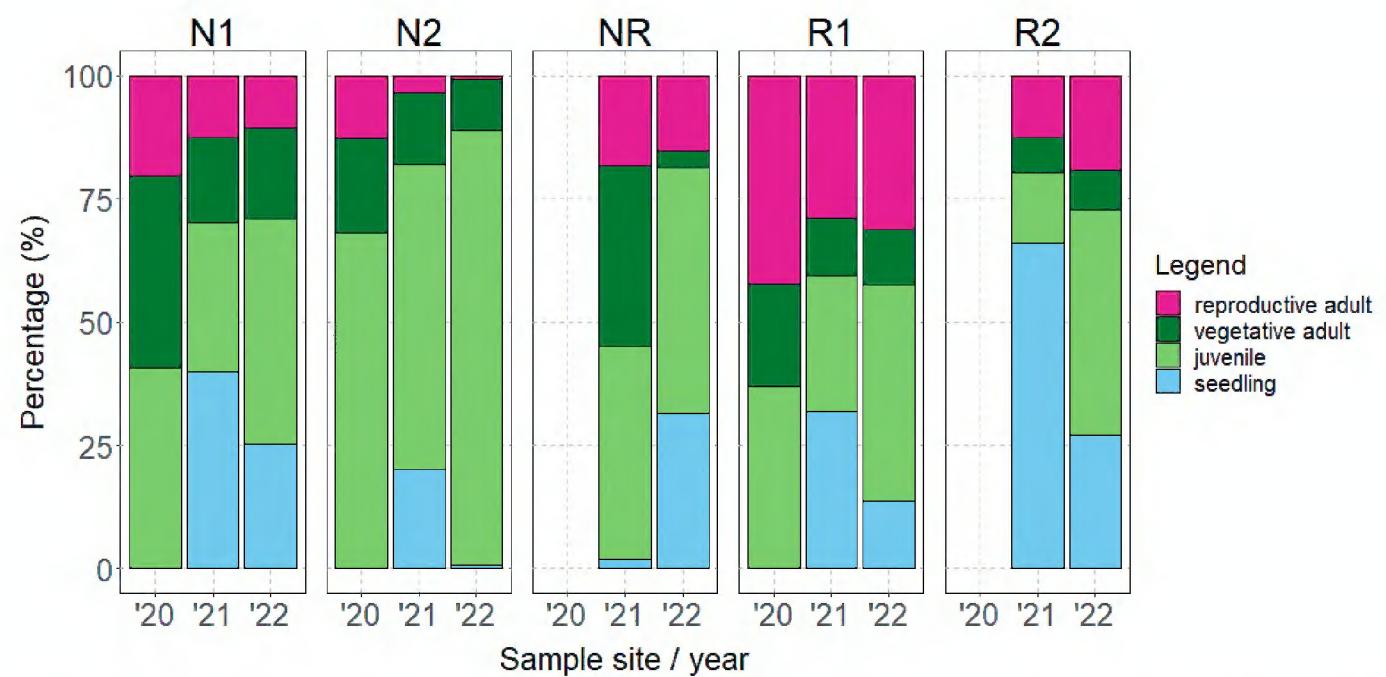
Numerical analyses (descriptive statistics and one-way ANOVA with post-hoc Tukey-tests) were carried out using IBM SPSS 22.0 and R version 4.1 (R Core Team 2015). The figures presented in this paper were prepared with R and ggplot2 package (version 3.4.2). Calculation of deterministic growth rates ( $\lambda$ ) was done in R with package popbio (version 2.7, Stubben and Milligan 2007).

## Results

The number of individuals present at a sample site showed notable changes between years (Table 1), which is partly due to individuals which did not appear aboveground in some years (we found such plants in all sites and in all years after the baseline survey), but more influenced by the high fluctuations in the number of seedlings each year. In 2020 there were no seedlings present in the surveyed quadrats, we found only a very few around the sample sites. In contrast, at most sites, in 2021 a high number of seedlings appeared which was followed by a lower, but still considerable amount in 2022. Only the NR site showed a different trend, where the number of seedlings was higher in 2022 (Fig. 1).



**Figure 1.** Population structure at each sample site between 2020 and 2022, seedlings included.



**Figure 2.** Population structure at each sample site between 2020 and 2022 with the exclusion of seedlings.

With the highly fluctuating seedlings category omitted, the population structure at each sample site during the three years show some uniform trends (Fig. 2). The fraction of juvenile individuals gradually increased at all sample sites during the study years. This was mainly caused by the substantial increase in the number of juvenile individuals, but in the case of N1, N2 and NR the decrease in the numbers of vegetative and reproductive adult individuals also contributed to this rearrangement in population structure. At sites with *Robinia pseudoacacia* dominance (R1, R2) the proportion of reproductive adults in the population and the ratio of vegetative/reproductive adults were notably higher than at sites with native tree species (N1, N2) for each year. The population structure of *E. dens-canis* population in native-Robinia mix stands (NR) was similar to native sites (N1, N2) in 2021, while in 2022 it was close to *Robinia* dominated sites (R1, R2).

Although seedling lengths were quite similar in 2021 and 2022 at each sample site (Fig. 3), we found significant differences between different sites in both years. Sites separated into two groups by statistical analyses (one-way variance analysis followed by Tukey-tests), with the R1 and R2 sites together with

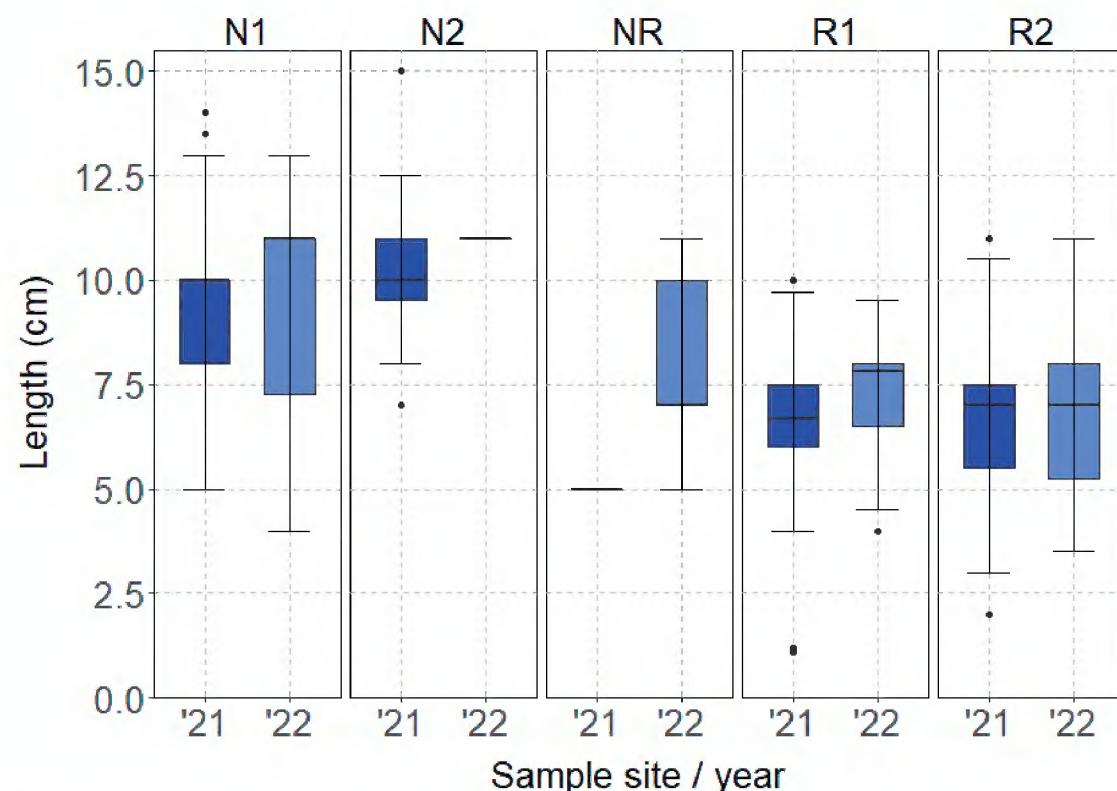


Figure 3. Length of seedlings at each sample site between 2021 and 2022.

**Table 2.** Number of cases (N) and means of vegetative characteristics of different age-states at the five sample sites between 2020 and 2022. The grouping results of ANOVA followed by Tukey tests is indicated in uppercase.

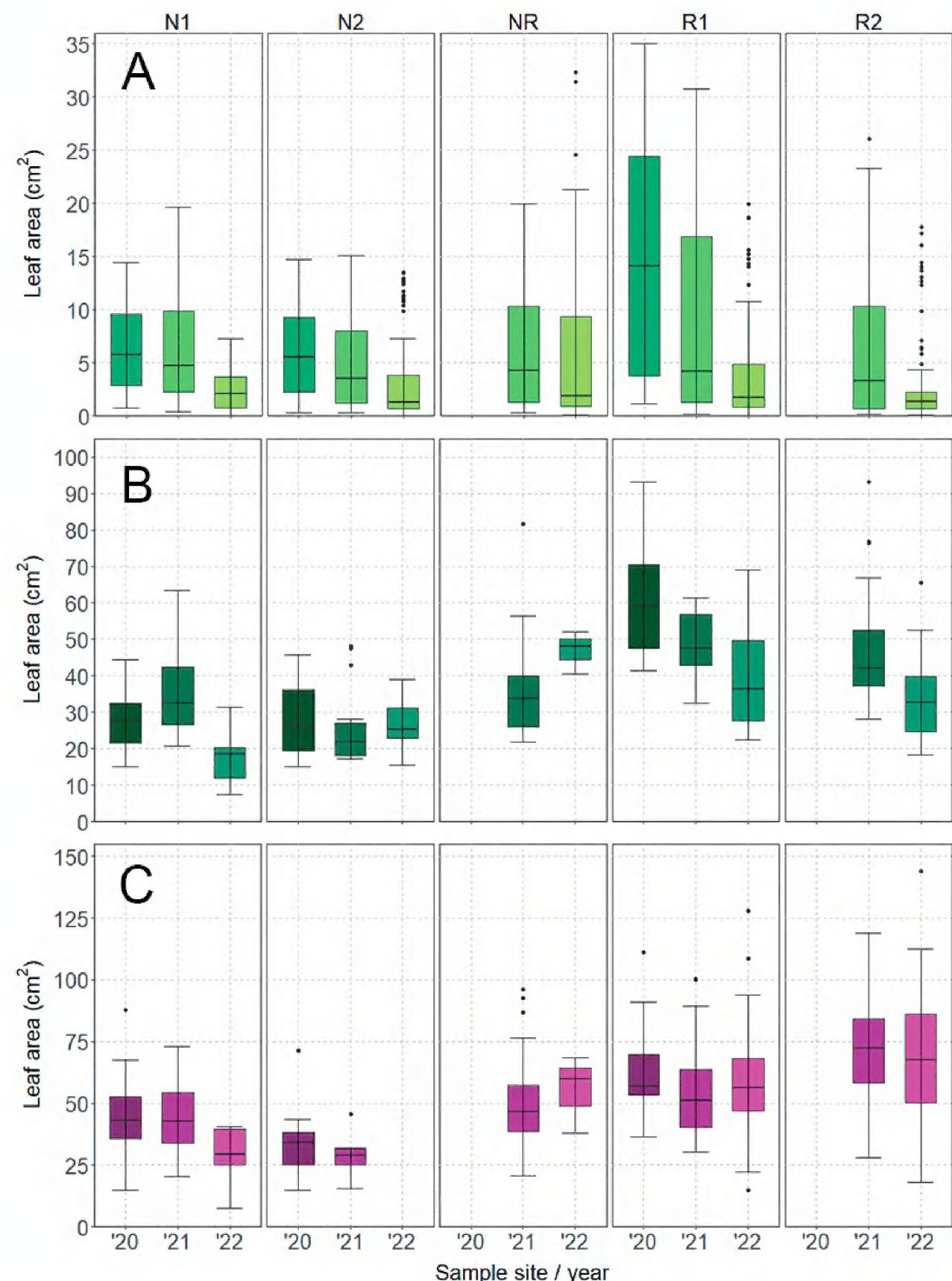
|   | Year | N1 |                     | N2  |                     | NR   |                     | R1 |                     | R2   |                     |
|---|------|----|---------------------|-----|---------------------|------|---------------------|----|---------------------|------|---------------------|
|   |      | N  | Mean                | N   | Mean                | N    | Mean                | N  | Mean                | N    | Mean                |
| Seedling length (cm)                            | 2020 | 0  | –                   | 0   | –                   | n.a. | n.a.                | 0  | –                   | n.a. | n.a.                |
|   | 2021 | 74 | 93.74 <sup>b</sup>  | 35  | 98.86 <sup>b</sup>  | 2    | 50.00 <sup>a</sup>  | 63 | 66.83 <sup>a</sup>  | 266  | 66.47 <sup>a</sup>  |
|   | 2022 | 26 | 96.35 <sup>b</sup>  | 0   | –                   | 27   | 79.82 <sup>a</sup>  | 28 | 71.29 <sup>a</sup>  | 99   | 70.95 <sup>a</sup>  |
| Juveniles leaf area (cm <sup>2</sup> )          | 2020 | 40 | 6.17 <sup>a</sup>   | 75  | 6.10 <sup>a</sup>   | n.a. | n.a.                | 36 | 15.45 <sup>b</sup>  | n.a. | n.a.                |
|   | 2021 | 56 | 6.50 <sup>ab</sup>  | 107 | 4.95 <sup>a</sup>   | 45   | 6.42 <sup>ab</sup>  | 60 | 8.72 <sup>b</sup>   | 57   | 6.81 <sup>ab</sup>  |
|   | 2022 | 48 | 2.50 <sup>a</sup>   | 128 | 3.06 <sup>a</sup>   | 43   | 6.23 <sup>b</sup>   | 89 | 4.13 <sup>a</sup>   | 167  | 2.43 <sup>a</sup>   |
| Vegetative adult leaf area (cm <sup>2</sup> )   | 2020 | 38 | 28.10 <sup>a</sup>  | 21  | 27.50 <sup>a</sup>  | n.a. | n.a.                | 20 | 60.69 <sup>b</sup>  | n.a. | n.a.                |
|   | 2021 | 32 | 34.39 <sup>b</sup>  | 25  | 25.13 <sup>a</sup>  | 38   | 35.33 <sup>b</sup>  | 17 | 48.85 <sup>c</sup>  | 29   | 47.56 <sup>c</sup>  |
|   | 2022 | 19 | 17.70 <sup>a</sup>  | 15  | 26.78 <sup>ab</sup> | 3    | 46.95 <sup>c</sup>  | 23 | 39.14 <sup>bc</sup> | 29   | 34.27 <sup>bc</sup> |
| Reproductive adult leaf area (cm <sup>2</sup> ) | 2020 | 19 | 44.92 <sup>a</sup>  | 9   | 35.44 <sup>a</sup>  | n.a. | n.a.                | 37 | 60.82 <sup>b</sup>  | n.a. | n.a.                |
|   | 2021 | 22 | 43.46 <sup>ab</sup> | 5   | 29.39 <sup>a</sup>  | 19   | 51.69 <sup>bc</sup> | 56 | 52.74 <sup>bc</sup> | 50   | 71.33 <sup>c</sup>  |
|   | 2022 | 8  | 28.63 <sup>a</sup>  | 0   | –                   | 3    | 55.48 <sup>ab</sup> | 58 | 58.01 <sup>b</sup>  | 64   | 68.53 <sup>b</sup>  |

NR forming one ( $p = 0.201$  in 2021 and  $0.177$  in 2022) and N1 and N2 sites forming the other in 2021 ( $p = 0.966$ ). In 2022 the latter group consisted of only N1 since the absence of seedlings at N2 in that year (Table 2).

Leaf areas of juvenile plants showed a similar decreasing trend in all sample sites during the three years (Fig. 4), most remarkably in R1. Although in 2021 and 2022 there were marked differences between the maximums of leaf areas, their means were much closer to each other (Table 2).

In the case of adult individuals (both vegetative and reproductive), their leaf areas were the largest at R1 and R2 sites, followed by NR, while the two sites with natural habitats had the smallest leaves in all three years. The extent of these differences varied between years (Table 2).

In all three sample sites which were surveyed over the three years, in 2022 we found adult individuals (10 vegetative and 2 reproductive) which were not



**Figure 4.** Leaf area of juvenile (**A**), vegetative adult (**B**) and reproductive adult (**C**) individuals at each sample site between 2020 and 2022.

recorded before, which suggests that *E. dens-canis* could become dormant for at least two years. Transition matrices also reveal that all age-states are prone to dormancy (Suppl. material 1). At sites with *Robinia*, reproductive plants had much higher tendency to flower again in subsequent years (32–86%) and juvenile plants developed into vegetative adult category in higher percentage. In terms of recruitment we did not observe notable trends as the rate of recruitment at each site varied greatly in some cases. The overall growth rates ( $\lambda$ ) of the populations also show some differences between sites (Table 3). During the first transition (2020–21) the one site with *Robinia* cover (R1) had the lowest growth rate by far (0.792) of the three surveyed sites, the two populations situated in native forest stands (N1, N2) had a  $\lambda$  close to 1 which is a characteristic of stable populations. However, during the 2021–2022 transition, this trend reversed, the two populations under *Robinia* (R1, R2) had the highest growth rate, while the ones under native stands (N1 and N2) had the lowest (still close to 1) and the mixed stand (NR) had a  $\lambda$  between the values of these two groups.

**Table 3.** Projected population growth rates ( $\lambda$ ) of each site.

| Sample site                    | 2020–2021 | 2021–2022 |
|--------------------------------|-----------|-----------|
| <b>Native 1 (N1)</b>           | 0.929     | 1.046     |
| <b>Native 2 (N2)</b>           | 0.978     | 1.001     |
| <b>Native-Robinia mix (NR)</b> | –         | 1.067     |
| <b>Robinia 1 (R1)</b>          | 0.792     | 1.128     |
| <b>Robinia 2 (R2)</b>          | –         | 1.365     |

## Discussion

Between 2020 and 2022 the number of individuals surveyed in the quadrats at sites with native tree species were more constant than at sites with *R. pseudoacacia*. These differences were mainly caused by the more pronounced recruitment in some years at the latter sites. Besides this difference in most sites the gradual increasing proportion of juvenile individuals in the populations was observed. Comparing the demographic characteristics of the studied populations with literature data we found that at the N1 and N2 site the demography of the *Erythronium* populations is very similar to what Kricsfalussy et al. (1995) described as “left-sided”, which means the dominance of young individuals, the highly dynamic seedling category and marginal proportion of adult plants in the populations. The populations situated in mixed forests showed somewhat similar trends, but with the growing proportion of *Robinia* in the forest stands (NR, R2, R1) the demographic distributions of the *Erythronium* populations gradually changing towards the “right-handed” state described by Kricsfalussy et al. (1995) with the difference that the seedling category is also significant and highly fluctuating. Despite the fact that prolonged dormancy (not producing aboveground shoots during one or more growing seasons even though the plant is still alive) has been reported in several genera of the lily family (Tyler and Borchert 2002; Delvallée et al. 1990; Miller et al. 2004; Tatarenko 2019), we found no mention in the literature about the observation of this phenomenon regarding any species of the genus *Erythronium*. We found only mention of ‘senescent’ plants by Kricsfalussy et al. (1995) as old, dying bulbs without leaves. In contrast, at all sites in both years after the baseline survey we found individuals from multiple age-states which were not present aboveground in the previous one or two years. The relatively high number of such plants indicates that this phenomenon is most likely not only the result of occasional damage occurring to plants, but a natural characteristic of the species.

The average size of adult individuals was significantly greater in the populations under *Robinia* than at the sites in native forests in all three years. Such a difference would hardly be explained by the location, exposure or geology of the sample sites, and it is therefore assumed that differences in the composition of the forest stands in the sample sites may be the cause of this phenomenon. It is known that *R. pseudoacacia* can significantly increase the amount of nitrogen available for uptake by *Rhizobium* bacteria (Rice et al. 2004), often resulting in a significant increase in the leaf area of species in its understory (Guo et al. 2021).

Although the mean of leaf areas of juvenile plants decreased in all areas throughout the three years, the lower limit of the leaf area of reproductive

individuals did not change as much. Thus, even smaller plants became adults in each following year, which could be the result of gradual environmental changes or just a coincidence in weather patterns.

One transition does not tell much about recruitment or growth rate of the population (Crawley 1990), as these values are highly variable, likely depending on environmental factors among others as well. However, it is notable that although the  $\lambda$  value of the one population under *Robinia* (R1) during the 2020–21 transition was the lowest among all sites, in the next transition the  $\lambda$  values of *Robinia* stands were the highest by far. The populations situated in native stands had a similar growth rate (close to 1) in both transitions. As in 2020 we could not find any seedlings in any surveyed quadrats, and in 2021 and 2022 there were numerous in some sites, these great differences in recruitment rates likely caused by annual variances in weather. Great differences between recruitment rate at different sites have been observed in the case of this species (Kricsfalusi et al. 1987) but in our study these contrasts cannot be attributed to differences in geographical conditions as all our study sites are situated in the same landscape and the NR site which is just 50 metres in distance from the N1 site shows the highest similarities with the R2 site (9 km away). The low  $\lambda$  value of R1 in the 2020–21 transition means that the population without recruitment is rapidly declining even with the mortality rates omitted during the calculation of deterministic growth rates. In the 2021–22 transition the presence of recruitment made  $\lambda$  considerably higher than the 2020–21 value, which suggests that in *Robinia*-dominated habitat type *E. dens-canis* is highly relying on recruitment and these populations could be characterized by a more dynamic demography which is generally uncommon in long-lived herbaceous species (Eriksson 1989), but not unknown for *E. dens-canis* (Kricsfalusi et al. 1995).

In contrast with the R1 and R2 populations, the *E. dens-canis* populations situated in native forests have more stable demographical characteristics, their growth rate was close to 1 with or without recruitment. The *Robinia*-native tree species mixed stand (NR) showed an intermediate growth rate, which also suggests that the greater the ratio of *Robinia* in a stand the greater is its effect on the *Erythronium* population as well. Since these values were also calculated without the mortality rates of most age-states, the growth rates are likely lower. It could easily change the growth rate of populations in native forest stands from stable or slowly growing to a declining category.

## Conclusions

Nitrogen pollution originating from agricultural activities (fertilization, production of leguminous crops) is a common potential threat to biodiversity, especially to endangered species (Hernández et al. 2016). The habitat-transforming capability of *R. pseudoacacia* is already known, which is mostly caused by increasing nitrogen input into the ecosystem (Buzhdyan et al. 2016; Vítková et al. 2016), however its effect on endangered plant species is a less studied topic. Our results agree with previous studies (Buzhdyan et al. 2016) that *R. pseudoacacia* accelerates environmental processes, as *E. dens-canis* populations under *R. pseudoacacia* show much more volatile deterministic growth rates and higher turnover compared with populations situated under native tree

species and this effect was greater in sites with greater ratio of *Robinia* in the tree cover. Such variations in the life cycle of plants may support the dynamic heterogeneity of populations which in turn ensures their stability in different environmental conditions and management regimes (Kricsfalusi 2016). In most aspects, where we found differences among populations, the extent of these differences was in correlation with the proportion of *R. pseudoacacia* in the forest stands, as the population at the NR site often showed intermediate characteristics between the native and *Robinia*-dominated stands.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: JB, BP. Data curation: VL, BP, EAB. Formal analysis: BP. Funding acquisition: JB. Investigation: BF, EAB, BP, VL. Methodology: JB. Project administration: JB. Resources: EAB. Supervision: JB. Validation: VL, BF. Visualization: BP. Writing – original draft: BP, JB. Writing – review and editing: JB, BP.

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### Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

## References

Bagi I, Kovács G, Székely Á (1998) A *Crocus reticulatus* Stev. Előfordulása a kunfehérvári holdrutás erdőben. Kitaibelia 3(2): 231–233. [in Hungarian]. [http://kitaibelia.unideb.hu/articles/Kitaibelia\\_vol32\\_p231-233.pdf](http://kitaibelia.unideb.hu/articles/Kitaibelia_vol32_p231-233.pdf)

Brana S, Vukovic N, Kaligarić M (2014) Least adder's-tongue (*Ophioglossum lusitanicum* L.) in Croatia – distribution, ecology and conservation. Acta Botanica Croatica 73(2): 471–480. <https://doi.org/10.2478/botcro-2014-0015>

Buzhdyan OY, Rudenko SS, Kazanci C, Patten BC (2016) Effect of invasive black locust (*Robinia pseudoacacia* L.) on nitrogen cycle in floodplain ecosystem. Ecological Modelling 319: 170–177. <https://doi.org/10.1016/j.ecolmodel.2015.07.025>

Celesti-Grapow L, Pretto F, Brundu G, Carli E, Blasi C (2009) A Thematic Contribution to the National Biodiversity Strategy. Plant Invasion in Italy, an Overview. Ministry for the Environment Land and Sea Protection, Nature Protection Directorate, Roma, 36 pp. [https://www.mase.gov.it/sites/default/files/archivio/biblioteca/protezione\\_natura/dpn\\_plant\\_invasion\\_italy.pdf](https://www.mase.gov.it/sites/default/files/archivio/biblioteca/protezione_natura/dpn_plant_invasion_italy.pdf)

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, von der Lippe M, Weber E (2013) Biological flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology 101(6): 1623–1640. <https://doi.org/10.1111/1365-2745.12162>

Crawley MJ (1990) The population dynamics of plants. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 330(1257): 125–140. <https://doi.org/10.1098/rstb.1990.0187>

Daehler CC, Strong DR (1994) Native plant biodiversity vs. The introduced invaders: status of the conflict and future management options. In: Majumdar SK, Brenner FJ, Lovich JE, Schalles JF, Miller EW (Eds) Biological Diversity: Problems and Challenges. Pennsylvania Academy of Science, Easton, PA, 92–113.

De Marco A, Arena C, Giordano M, De Santo AV (2013) Impact of the invasive tree black locust on soil properties of Mediterranean stone pine-holm oak forests. Plant and Soil 372(1–2): 473–486. <https://doi.org/10.1007/s11104-013-1753-6>

Delvallée I, Paffen A, De Klerk GJ (1990) The development of dormancy in bulblets of *Lilium speciosum* generated in vitro. 2. The effect of temperature. Physiologia Plantarum 80(3): 431–436. <https://doi.org/10.1111/j.1399-3054.1990.tb00063.x>

Didham RK, Tylianakis JM, Gemmell NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification on species invasion and native species decline. Trends in Ecology & Evolution 22(9): 489–496. <https://doi.org/10.1016/j.tree.2007.07.001>

Eriksson O (1989) Seedling dynamics and life histories in clonal plants. Oikos 55(2): 231–238. <https://doi.org/10.2307/3565427>

FOEN [Federal Office for the Environment] (2010) Switzerland's Fourth National Report under the Convention on Biological Diversity. Swiss Confederation, Bern, 132 pp. <https://www.cbd.int/doc/world/ch/ch-nr-04-en.pdf>

Gaertner M, Den Breeyen A, Hui C, Richardson DM (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: A meta-analysis. Progress in Physical Geography 33(3): 319–338. <https://doi.org/10.1177/0309133309341607>

Gederaas L, Loennechen Moen T, Skjelseth S, Larsen LK (2012) Alien species in Norway – with the Norwegian Black List 2012. The Norwegian Biodiversity Information Centre (NBIC), Norway, 214. [https://www.artsdatabanken.no/Files/13960/Alien\\_Species\\_in\\_Norway\\_-\\_with\\_the\\_Norwegian\\_Black\\_List\\_2012](https://www.artsdatabanken.no/Files/13960/Alien_Species_in_Norway_-_with_the_Norwegian_Black_List_2012)

Göhre K (1952) Die Robinie Und Ihr Holz. Deutscher Bauernverlag, Berlin, 287–326.

Gutián J, Gutián P, Medrano M, Sanchez JM (1999) Variation in floral morphology and individual fecundity in *Erythronium dens-canis* (Liliaceae). Ecography 22(6): 708–714. <https://doi.org/10.1111/j.1600-0587.1999.tb00520.x>

Gutián P, Medrano M, Gutián J (2003) Seed dispersal in *Erythronium dens-canis* L. (Liliaceae): Variation among habitats in a myrmecochorous plant. Plant Ecology 169(2): 171–177. <https://doi.org/10.1023/A:1026043411357>

Guo Q, Wen Z, Zheng C, Li W, Fan Y, Zhu D (2021) Effects of *Robinia pseudoacacia* on the undergrowth of herbaceous plants and soil properties in the Loess Plateau of China. Journal of Plant Ecology 14(5): 896–910. <https://doi.org/10.1093/jpe/rtab041>

Hejda M, Pyšek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Plant Ecology* 132: 143–152. <https://doi.org/10.1007/s11258-018-0898-z>

Hernández DL, Vallano DM, Zavaleta ES, Tzankova Z, Pasari JR, Weiss S, Selmants PC, Morozumi C (2016) Nitrogen pollution is linked to US listed species declines. *Bioscience* 66(3): 213–222. <https://doi.org/10.1093/biosci/biw003>

Holland PG (1974) The growth behavior, ecology, and geography of *Erythronium americanum* in northeast North America. *Canadian Journal of Botany* 52(7): 1765–1772. <https://doi.org/10.1139/b74-228>

Holland PG (1980) Trout lily in Nova Scotia: An assessment of the status of its geographic range. *Journal of Biogeography* 7(4): 363–381. <https://doi.org/10.2307/2844656>

Holland PG (1981) The demography of trout lily (*Erythronium americanum* Ker.) in Nova Scotia. *Vegetatio* 45(2): 97–106. <https://doi.org/10.1007/BF00119219>

Hruška K (1991) Human impact on the forest vegetation in the western part of the Pannonic Plain (Yugoslavia). *Vegetatio* 92(2): 161–166. <https://doi.org/10.1007/BF00036036>

Hughes JW (1992) Effect of removal of co-occurring species on distribution and abundance of *Erythronium americanum* (Liliaceae), a spring ephemeral. *American Journal of Botany* 79(12): 1329–1336. <https://doi.org/10.2307/2445130>

Hurdu BI, Coste A, Halmagyi A, Szatmari PM, Farkas A, Puşcaş M, Turtureanu PD, Rosca-Căsian O, Tanase C, Oprea A, Mardari C, Radutoiu D, Camen-Comanescu P, Sirbu I-M, Stoie A, Lupoae P, Cristea V, Jarda L, Holobiuc I, Goia I, Butiuc-Keul A (2022) Ex situ conservation of plant diversity in Romania: A synthesis of threatened and endemic taxa. *Journal for Nature Conservation* 68: 126211. <https://doi.org/10.1016/j.jnc.2022.126211>

Jeong H, Cho YC, Kim E (2022) Site-specific temporal variation of population dynamics in subalpine endemic plant species. *Scientific Reports* 12: 19207. <https://doi.org/10.1038/s41598-022-23903-5>

Kawano S (2005) Life-history monographs of Japanese plants. 1: *Erythronium japonicum* Decne. (Liliaceae). *Plant Species Biology* 20(1): 67–74. <https://doi.org/10.1111/j.1442-1984.2005.00125.x>

Kawano S, Takasu H, Nagai Y (1978) The productive and reproductive biology of flowering plants. IV. Assimilation behaviour of some temperate woodland herbs. *Journal of Liberal Arts and Humanities, Toyama Univ. Japan.* 11: 33–60. <https://doi.org/10.1007/BF00540197>

Kawano S, Hiratsuka A, Hayashi K (1982) Life history characteristics and survivorship of *Erythronium japonicum*. The productive and reproductive biology of flowering plants V. *Oikos* 38(2): 129–149. <https://doi.org/10.2307/3544013>

Király G (2007) Vörös Lista. A magyarországi edényes flóra veszélyeztett fajai. Red list of the vascular flora of Hungary. Private edition, Sopron, 73 pp.

Király G ([ed.]) 2009) Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcsok. ANP Igazgatóság, Jósvafő, 616 pp. [in Hungarian]

Kricsfalusy M (2016) Variations in the life cycle of *Anemone patens* L. (Ranunculaceae) in wild populations of Canada. *Plants* 5(3): 29. <https://doi.org/10.3390/plants5030029>

Kricsfalusy M, Mihaly AV (1993) Chorological and ecology-phytocoenotic peculiarities of ephemeral geophytes of the Ukrainian Carpathians. *Ukrainskyi Botanichnyi Zhurnal* 50: 13–22. [in Russian]

Kricsfalusy M, Komendar VI, Mező-Kricsfalusi GN, Szabados VI, Fesenko SS, Shumskaya NV (1987) Study on reproductive biology of ephemerals in the Tisza River basin (Transcarpathia). *Tiscia* 22: 61–73. [in Russian]

Kricsfalussy M, Shushman V, Saroz OE (1995) Biomorphological and ecocoenotic characteristics of *Erythronium dens-canis* (Liliaceae) in the Carpathians. Botanicheskii Zhurnal 80: 35–52. [in Russian]

KSH (2023) A faállománnyal borított erdőterület és az élőfakészlet megoszlása fafa-jcsoportok és korosztályok szerint, december 31. (2000–). [https://www.ksh.hu/docs/hun/xstadat/xstadat\\_eves/i\\_ome002b.html](https://www.ksh.hu/docs/hun/xstadat/xstadat_eves/i_ome002b.html)

La Rocca N, Pupillo P, Puppi G, Rascio N (2014) *Erythronium dens-canis* L.: An unusual case of leaf mottling. Plant Physiology and Biochemistry 74: 108–117. <https://doi.org/10.1016/j.plaphy.2013.11.005>

McKinney ML, Lockwood JL (1999) Biotic homogenization: A few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14(11): 450–453. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)

Medina-Villar S, Castro-Díez P, Alonso A, Cabra-Rivas I, Parker IM, Pérez-Corona E (2015) Do the invasive trees, *Ailanthus altissima* and *Robinia pseudoacacia*, alter litterfall dynamics and soil properties of riparian ecosystems in Central Spain? Plant and Soil 396(1–2): 311–324. <https://doi.org/10.1007/s11104-015-2592-4>

Mihály B, Botta-Dukát Z (2006) Özönnövények: biológiai inváziók Magyarországon I. Budapest, 426 pp.

Miller MT, Antos JA, Allen GA (2004) Dormancy and flowering in two mariposa lilies (*Calochortus*) with contrasting distribution patterns. Canadian Journal of Botany 82(12): 1790–1799. <https://doi.org/10.1139/b04-144>

Mondoni A, Rossi G, Probert R (2012) Temperature controls seed germination and dormancy in the European woodland herbaceous perennial *Erythronium dens-canis* (Liliaceae). Plant Biology 14(3): 475–480. <https://doi.org/10.1111/j.1438-8677.2011.00517.x>

Montagnini F, Haines B, Swank WT (1991) Soil-solution chemistry in black locust, pine mixed-hardwoods and oak hickory forest stands in the Southern Appalachians, USA. Forest Ecology and Management 40(3–4): 199–208. [https://doi.org/10.1016/0378-1127\(91\)90039-X](https://doi.org/10.1016/0378-1127(91)90039-X)

Muller RN, Bormann FH (1976) Role of *Erythronium americanum* Ker. In energy flow and nutrient dynamics of a northern hardwood forest ecosystem. Science 193(4258): 1126–1128. <https://doi.org/10.1126/science.193.4258.1126>

Nagy T, Pfleigler WP, Takács A, Tökölyi J, Molnár VA (2019) Distribution, infection rates and DNA barcoding of *Uromyces erythronii* (Pucciniaceae), a parasite of *Erythronium* (Liliaceae) in Europe. Willdenowia 49(1): 13–20. <https://doi.org/10.3372/wi.49.49103>

Nascimbene J, Marini L (2010) Oak forest exploitation and black-locust invasion caused severe shifts in epiphytic lichen communities in Northern Italy. Science of The Total Environment 408: 5506–5512. <https://doi.org/10.1016/j.scitotenv.2010.07.056>

Niklfeld H, Schrott-Ehrendorfer L (1999) Rote Liste gefährdeter Farn-und Blütenpflanzen (Pteridophyta und Spermatophyta) Österreichs. 2. Fassung. Rote Listen gefährdeter Pflanzen Österreichs 2: 33–152. [in German]

Pacsai B, Fülöp B, Bódis J (2022) A kakasmandikó (*Erythronium dens-canis* L.) demográfiai kutatásának módszertani megalapozása. Botanikai Közlemények 109(2): 201–217. [in Hungarian] <https://doi.org/10.17716/BotKozlem.2022.109.2.201>

Peloquin RL, Hiebert RD (1999) The effects of black locust (*Robinia pseudoacacia* L.) on species diversity and composition of black oak savanna/woodland communities. Natural Areas Journal 19: 121–131.

Pergl J, Sádlo J, Petrusk A, Laštůvka Z, Musil J, Perglová I, Šanda R, Šefrová H, Šíma J, Vohralík V, Pyšek P (2016) Black, Grey and Watch Lists of alien species in the Czech

Republic based on environmental impacts and management strategy. *NeoBiota* 28: 1–37. <https://doi.org/10.3897/neobiota.28.4824>

Perrino EV, Ladisa G, Calabrese G (2014) Flora and plant genetic resources of ancient olive groves of Apulia (Southern Italy). *Genetic Resources and Crop Evolution* 61(1): 23–53. <https://doi.org/10.1007/s10722-013-0013-1>

Perrino EV, Tomaselli V, Wagensommer RP, Silletti GN, Esposito A, Stinca A (2022) *Ophioglossum lusitanicum* L.: New Records of Plant Community and 92/43/EEC Habitat in Italy. *Agronomy (Basel)* 12(12): 3188. <https://doi.org/10.3390/agronomy12123188>

Perrino EV, Mahmoud ZNA, Valerio F, Tomaselli V, Wagensommer RP, Trani A (2023) Synecology of *Lagoecia cuminoides* L. in Italy and evaluation of functional compounds presence in its water or hydroalcoholic extracts. *Scientific Reports* 13(1): 20906. <https://doi.org/10.1038/s41598-023-48065-w>

Pimentel D, McNair S, Janecka J, Wightman J, Simmonds C, O'Connell C, Wong E, Russel L, Zern J, Aquino T, Tsomondo T (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems & Environment* 84(1): 1–20. [https://doi.org/10.1016/S0167-8809\(00\)00178-X](https://doi.org/10.1016/S0167-8809(00)00178-X)

Pupillo P, Astuti G (2017) Population structure of *Erythronium dens-canis* L. (Liliaceae) in the northern Apennines (Italy). *Italian Botanist* 4: 1–14. <https://doi.org/10.3897/ib.4.12439>

Pyšek P, Danihelka J, Sádlo J, Chrtek Jr J, Chytrý M, Jarošík V, Kaplan Z, Krahulec F, Moravcová L, Pergl J, Štajerová K, Tichý L (2012) Catalogue of alien plants of the Czech Republic (2<sup>nd</sup> edition): checklist update, taxonomic diversity and invasion patterns. *Preslia* 84: 155–255. <https://www.preslia.cz/P122Pysek.pdf>

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

Rabotnov TA (1985) Dynamics of Plant Coenotic Populations. In: White J (Ed.) *The Population Structure of Vegetation. Handbook of Vegetation Science*, vol 3. Springer, Dordrecht, 121–142. [https://doi.org/10.1007/978-94-009-5500-4\\_6](https://doi.org/10.1007/978-94-009-5500-4_6)

Rice SK, Westerman B, Federici R (2004) Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen-cycling in a pine–oak ecosystem. *Plant Ecology* 174(1): 97–107. <https://doi.org/10.1023/B:VEGE.0000046049.21900.5a>

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive species – A global review. *Diversity & Distributions* 17(5): 788–809. <https://doi.org/10.1111/j.1472-4642.2011.00782.x>

Rooney TP, Wiegmann SM, Rogers DA, Waller DM (2004) Biotic impoverishment and homogenization in unfragmented forest understory. *Conservation Biology* 18(3): 787–798. <https://doi.org/10.1111/j.1523-1739.2004.00515.x>

Ruhren S, Dudash MR (1996) Consequences of the timing of seed release of *Erythronium americanum* (Liliaceae), a deciduous forest myrmecochore. *American Journal of Botany* 83(5): 633–640. <https://doi.org/10.1002/j.1537-2197.1996.tb12749.x>

Sawada S, Chida S, Sawaguchi Y, Nagasawa N (1997) Dry matter production, population structure and environmental conditions of the spring ephemeral *Erythronium japonicum* growing in various habitats differing in sunlight exposure in cool temperate Japan. *Ecological Research* 12(1): 89–99. <https://doi.org/10.1007/BF02523614>

Seitz B, Nehring S (2013) Naturschutzfachliche Invasivitätsbewertung. *Robinia pseudoacacia* – Robinie. In: Nehring S, Kowarik I, Rabitsch W, Essl F (Eds) *Naturschutzfachliche Invasivitätsbewertungen für in Deutschland wild lebende gebietsfremde Gefäßpflanzen*. BfN-Schriften 352, Bundesamt für Naturschutz, Bonn, 168–169. [in German]

Sitzia T, Campagnaro T, Kotze DJ, Nardi S, Ertani A (2018) The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. *Scientific Reports* 8(1): 8410. <https://doi.org/10.1038/s41598-018-26493-3>

Straker KC, Quinn LD, Voigt TB, Lee DK, Kling GJ (2015) Black locust as a bioenergy feedstock: A review. *BioEnergy Research* 8(3): 1117–1135. <https://doi.org/10.1007/s12155-015-9597-y>

Stubben C, Milligan B (2007) Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 22(11): 1–23. <https://doi.org/10.18637/jss.v022.i11>

Takada T, Nakayama S, Kawano S (1998) A sensitivity analysis of the population dynamics of *Erythronium japonicum*, a liliaceous perennial. *Plant Species Biology* 13(2–3): 117–127. <https://doi.org/10.1111/j.1442-1984.1998.tb00253.x>

Taniguchi T, Kanzaki N, Tamai S, Yamanaka N, Futai K (2007) Does ectomycorrhizal fungal community structure vary along a Japanese black pine (*Pinus thunbergii*) to black locust (*Robinia pseudoacacia*) gradient? *The New Phytologist* 173(2): 322–334. <https://doi.org/10.1111/j.1469-8137.2006.01910.x>

Tatarenko I (2019) Having a break: Prolonged dormancy observed in a rare species, *Fritillaria meleagris*. *Environment and Human: Ecological Studies* 9(3): 302–324. <https://doi.org/10.31862/2500-2961-2019-9-3-302-324>

Tessier JT (2019) Early spring warming may hasten leaf emergence in *Erythronium americanum*. *American Journal of Botany* 106(10): 1392–1396. <https://doi.org/10.1002/ajb2.1367>

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D (2001) Forecasting agriculturally driven global environmental change. *Science* 292(5515): 281–284. <https://doi.org/10.1126/science.1057544>

Turis P, Kliment J, Feráková V, Dítě D, Eliáš P, Hrvnák R, Koštál J, Šuvada R, Mráz P, Bernátová D (2014) Red List of vascular plants of the Carpathian part of Slovakia. *Thaiszia Journal of Botany* 24(1): 35–87.

Tykhonenko YY, Sytschak NN, Kagalo AA, Orlov OO (2017) New records of *Uromyces erythronii* (Pucciniales) from Ukraine. Ukrains'kyi Botanichnyi Zhurnal. Ukrains'ke Botanichne Tovarystvo 74(2): 184–188. <https://doi.org/10.15407/ukrbotj74.02.184>

Tyler C, Borchert M (2002) Reproduction and growth of the chaparral geophyte, *Zigadenus fremontii* (Liliaceae), in relation to fire. *Plant Ecology* 165(1): 11–20. <https://doi.org/10.1023/A:1021460025277>

Vacek S, Linda R, Králíček I, Vančura K, Prokůpková A, Prausová R (2020) Effect of structure and dynamics of forests on the occurrence of *Erythronium dens-canis*. *Journal of Forest Science* 66(9): 349–360. <https://doi.org/10.17221/96/2020-JFS>

Vadas E (1914) Die Monographie Der Robinie Mit Besonderer Rücksicht Auf Ihre Forstwirtschaftliche Bedeutung. Verlag August Joerges WWE & Sohn, Selmecbánya, 252 pp.

Vilá M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8(3): 134–144. <https://doi.org/10.1890/080083>

Vítková M, Pergl J, Sádlo J (2016) Black locust: from global ecology to local management – a case study from the Czech Republic. In: Krumm F, Vítková L (Eds) *Introduced tree species in European forests: opportunities and challenges*. European Forest Institute, 423 pp. [http://in-tree.org/uploads/images/book/Introduced\\_tree\\_species\\_EN\\_HighRes.pdf](http://in-tree.org/uploads/images/book/Introduced_tree_species_EN_HighRes.pdf)

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. *Forest Ecology and Management* 384: 287–302. <https://doi.org/10.1016/j.foreco.2016.10.057>

Von Holle B, Joseph KA, Largay EF, Lohnes RG (2006) Facilitations between the introduced nitrogen-fixing tree, *Robinia pseudoacacia*, and nonnative plant species in the glacial outwash upland ecosystem of cape cod, MA. *Biodiversity and Conservation* 15(7): 2197–2215. <https://doi.org/10.1007/s10531-004-6906-8>

Wendelberger G (1954) Die Robinie in den kontinentalen Trockenwäldern Mittel und Osteuropas. *Allgemeine Forstzeit* 65: 237–239. [in German]

Yokoi Y (1976) Growth and reproduction in higher plants II. Analytical study of growth and reproduction of *Erythronium japonicum*. *Botanical Magazine Tokyo* 89(1): 15–31. <https://doi.org/10.1007/BF02489531>

## Supplementary material 1

### Transition matrices of *Erythronium dens-canis* populations between 2020 and 2022

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Data type: docx

Explanation note: Transition matrices of *Erythronium dens-canis* populations in five sample sites (2 in native forests, 2 in *Robinia pseudoacacia*-dominated stands and 1 in mixed, native-*Robinia* stands) in Hungary between 2020 and 2022.

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